

Review

The Role of Cryptogams in Soil Property Regulation and Vascular Plant Regeneration: A Review

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Abstract: Despite their small size, cryptogams (lichen, liverwort, and moss) are important for ecosystem stability. Due to their strong stress resistance, cryptogams often cover extreme environments uninhabitable for vascular plants, which has an important impact on the material cycle and energy flow of various terrestrial ecosystems. In this article, we review and discuss the effects of cryptogams on soil properties (moisture and fertility) and vascular plant regeneration over the past two decades. Cryptogams strongly affect soil water content by influencing precipitation infiltration, non-rainfall water input, soil evaporation, soil water holding capacity, and soil permeability, ultimately helping to reduce soil water content in areas with low annual precipitation (<500 mm). However, in areas with high annual precipitation (>600 mm) or where the soil has other water sources, the presence of cryptogams is conducive to soil water accumulation. Cryptogam plants can increase soil fertility and the availability of soil nutrients (TOC, TN, TP, TK, and micronutrients) in harsh environments, but their effects in mild environments have not been sufficiently investigated. Cryptogam plants exert complex effects on vascular plant regeneration in different environments. The primary influence pathways include the physical barrier of seed distribution, shading, allelopathy, competition, influences on ectomycorrhizal development and individual reproduction, and the regulation of soil water content, temperature, and nutrients.

Keywords: moss; lichen; soil water content; soil fertility; vascular plant regeneration



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1. Introduction

Cryptogams (lichen, liverwort, and moss) [1] are widely distributed on Earth and can be found in arid, humid, cold, and hot climates [2]. They simultaneously exert their ecological effects in a variety of environments on Earth. However, they often produce different or even diametrically opposed ecological effects in different studies. For example, a large number of studies have found that a cryptogam presence leads to increased soil water loss and thus reduces soil water content [3–7]. However, there are also a considerable number of studies on the accumulation of soil water caused by cryptogam [8–10]. In addition, a great deal of research has also found that cryptogams cause changes in soil water distribution in different soil layers [10–13]. This involves the influence of cryptogam on non-rainfall water input, evaporation, soil infiltration capacity, water-holding capacity, water diffusion capacity, and water absorption capacity. In most cases, soils covered with cryptogams have higher fertility, such as OM [14,15], TOC [16,17], TN [18,19], TP [20,21], and TK [22,23], not to mention higher nutrient availability [24–27]. However, it has also been found that lichen leads to a decrease in soil OM content [28], moss reduces the availability of soil N [29], and moss crust leads to a reduction in phosphorus available [14]. The accelerated weathering of the parent material and the special life activities of moss will also release many micronutrients (Fe, Ca, Mg, Na, Cu, and Zn) into the soil [30,31], resulting in an increase in micronutrient content.

There are many ways in which cryptogams can affect vascular plant regeneration, and the results are varied. A large quantity of research exists discussing the physical barrier effect [32], allelopathy [33], and the indirect effects of cryptogams on vascular plant regeneration through their impact on soil [34]. The physical barrier effect of cryptogam is that the thick and dense cryptogam layer can limit the entry of vascular plant seeds [32] or light [35] into the soil, resulting in the failure of regeneration. The allelopathy of cryptogam plants refers to the effect of their secondary metabolites on seed germination and seedling growth in vascular plants [36]. Soil water content, nutrient content, and soil temperature have important effects on seed germination and seedling growth of vascular plants [26,37]. However, cryptogam often leads to changes in soil moisture [10], nutrient [17] content, and soil temperature [38], indirectly affecting the regeneration of vascular plants. In addition, in some other studies, cryptogams have also influenced growth and reproduction by competing with vascular plants [39], hindering the mycorrhizal infection of vascular plants [36], or limiting the reproductive capacity of individual vascular plants [19].

2. Effects of Cryptogam on Soil Properties

2.1. Effects of Cryptogam on Content and Vertical Distribution of Soil Water

Many studies suggest that cryptogams exert limiting effects on soil water infiltration [19,40]. In the study of Mu Us Sandy Land in China, it was found that a high coverage (100%) of moss crusts limited the infiltration rate and cumulative infiltration of rainwater and increased soil evaporation, leading to a decrease in soil moisture content. Additionally, reducing moss coverage to 40% did not significantly alleviate this effect on soil water content reduction [41]. Similar results were found in the study of the Loess Plateau, where scholars found that moss crust leads to a decrease in soil infiltration rate and cumulative infiltration [13]. In the study of Xiao et al., the soil water content was reduced due to the strong water-holding capacity of the moss layer [4]. In addition to the important effect of precipitation on soil water content, non-rainfall water is also an important water input for soils in drier regions [42]. Li's study found that moss crusts are able to intercept more non-rainfall water in the environment [43], but subsequent studies showed that bryophytes intercept non-rainfall water at a comparable rate to the increase in soil evaporation caused by it [44]. Zhang's research showed that lichen and moss crusts intercept a lot of dew due to their complex morphology and increased soil roughness. In addition, the authors discovered that soil under moss crusts cools faster at night, promoting the formation of dew. As such, the soil dew retention under different cover conditions manifests as moss crust > lichen crust > algae crust > bare soil [45].

The effect of cryptogam on soil water evaporation is another important cause of soil water change. In a study of the Loess Plateau wind–water erosion crisscross region in China, it was found that soils covered by moss crust had higher evaporation rates and cumulative evaporation capacity [7]. Conducting evaporation tests in both greenhouse and field environments, Kidron found that, in the greenhouse setting, when the water was fully absorbed by sandy soil, mosses with higher morphology and higher biomass were more conducive to the maintenance of soil water. However, under natural outdoor conditions, both cyanobacteria and moss crust increased the evaporation of sandy soil and reduced soil water content [46]. Zhang's study found similar results, discovering that when the soil water content is high, soil evaporation becomes weaker compared with bare soil moss crusting, which is conducive to the maintenance of soil water content. As evaporation progresses, in situations where the soil water content decreases to a certain level, moss crusts exercise the opposite effect, resulting in increased soil water loss [47]. One explanation for this phenomenon is that moss is not conducive to the transport of soil capillary water when the soil water content is high, and doing so will lead to a decrease in evaporation. In drier conditions, the unsaturated hydraulic conductivities of bare soil decreased rapidly, while those of moss-covered soil did not. This meant that the moss-covered soil maintained relatively high levels of evaporation, suggesting that

moss promotes soil water accumulation in humid environments, and dry conditions may exacerbate soil drought [48].

Cryptogams exert important effects on soil properties, including improving soil texture, increasing soil organic matter content [8], expanding soil water holding capacity [7,19], and elevating topsoil porosity and permeability [49], which results in a change in the vertical distribution of soil water. Xiao's study found that the moss-dominated biocrust increased the topsoil (0–5 cm) water content in semi-arid areas, decreased the soil water content by 15–50 cm, and had no effect on the deeper soil water content [12]. Sun et al. found that when the soil water content was the same, the moss crust caused a significant decrease in the soil water diffusion rate and adsorption ability, which led to the accumulation of water on the soil surface (0–10 cm). On the other hand, soil water content decreased in deep soil (10–20 cm) due to reduced water acquisition [13]. Through the artificial cultivation of biological crust in semi-arid areas, Xiao et al. found that the artificial moss crust increased the soil moisture content of the surface layer (0–20 cm) but seriously decreased the soil moisture content below 30 cm, leading to a decrease in the total soil moisture content on the whole. Overall, the longer the development time of the moss crust, the more obvious the reduction effect is [11]. However, other studies have reached the opposite result. Through an artificial rainfall simulation experiment, Kakeh found that lichen and moss crusts are conducive to precipitation infiltration into deeper soil [10].

The effect of cryptogams on soil water content seems to be regulated by precipitation or soil water content. In Li's simulated rainfall research, the increase in artificial rainfall led to a significant increase in the infiltration of deep soil water [40]. In Kidron's study, the average annual precipitation in the local area was only 95 mm. In the outdoor experiment, the presence of moss crust resulted in a decrease in soil water content. In petri dish experiments, the soil was saturated with water and then exposed to an environment identical to that of the outdoor experiment. In such scenarios, the moss causes the soil to retain more water [46]. Zhang et al.'s study also found that biological crust significantly reduced soil water content; however, on the gully floor with sufficient water, this reduction was significantly mitigated [50]. The above studies seem to imply that cryptogams are beneficial to the maintenance of soil water content in humid environments but will exacerbate soil and water loss in drought conditions. In the absence of artificial irrigation and other water sources, the boundary between humidity and drought seemed to be between 500–600 mm in terms of annual precipitation (Table 1). We speculate that the reason for this phenomenon was that a single precipitation was thin in the region with low precipitation. This may only be enough water to infiltrate the cortex and the surface soil, and it is often lost due to evaporation. In areas with high precipitation, rainfall successfully enters the soil layer in large quantities, and this part of the water is protected by better soil texture and more organic composition created by moss [8].

Table 1. Effect of cryptogam on soil water content in zone with different annual precipitation.

Geomorphic Feature	Cryptogam Species	Effects of Cryptogam on Soil Water Content	Annual Precipitation (mm)	References
Desert	Natural moss-dominated crusts	Decreasing	95	[46]
Desert	Natural moss-dominated crusts	Increasing	191 ^a	[47]
Plain	Lichens: <i>Psora decipiens</i> , <i>Diploschistes diacapsis</i> , <i>Collema tenax</i> , <i>Fulgensia bracteata</i> , <i>Squamarina cartilaginea</i> , <i>Toninia sedifolia</i> and <i>Caloplaca tominii</i> . Moss: <i>Tortula revolvens</i> , <i>Aloina bifrons</i> , <i>Aloina aloidas</i> and <i>Barbula trifaria</i>	Increasing	273 ^b	[10]

Table 1. Cont.

Geomorphic Feature	Cryptogam Species	Effects of Cryptogam on Soil Water Content	Annual Precipitation (mm)	References
Alpine steppe	Lichen–moss crusts and moss crusts	Decreasing	403.8	[6]
Wind–Water Erosion Crisscross Region	Cyanobacteria and moss biocrusts	Decreasing	409	[7]
Semiarid watershed on the Loess Plateau	Moss-dominated crust	Decreasing	409	[4,11]
The Loess Plateau	Biocrust with about 90% moss cover	Decreasing	409	[44]
Sandland	Natural moss-dominated crusts	Decreasing	440.8	[3,41]
The Loess Plateau	Moss-dorminate crust	Decreasing	505	[50]
Haleakala’s crater	<i>Grimmia trichophylla</i> and <i>Grimmia torquata</i>	Increasing	More than 600	[8]
Sand dune	Green algae crust, lichen–moss mat and moss mat	Increasing or having no effect	1100	[9]

^a: Although the local rainfall was very low, the soil fully absorbed water before the experiment, the soil water content was greatly increased, and the local rainfall could not reflect the soil water content level. ^b: The average annual rainfall in the area was only 273 mm; in the test, however, artificial rainfall was simulated for 90 min with a heavy rainfall of 40 mm per hour.

2.2. Effects of Cryptogam on Soil Fertility and Nutrients Availability

2.2.1. Effects of Cryptogam on Soil Organic Matter and Carbon Turnover

The primary sources of organic matter and carbon in soils are the secretions and dead residues of living plants [51]. In some harsh environments, such as deserts [15,16,25], sandy land [14], drylands [52], karst [20,21], waste tailings [53], and high-latitude [54] and high-altitude [55], most vascular plants are unable to survive. With cryptogam secretions, and dead residues as almost the only sources of soil C [2], cryptogams tend to increase soil C content in these areas. However, the rate of decomposition of moss crusts is very slow under the conditions of high temperature and low humidity in the desert [27]. Moreover, the effect of moss on soil C content is greater than that of lichen [23,26,55]. In alpine and high-latitude regions, the removal of moss crust directly leads to a decrease in TOC, DOC, and MBC content in soil, and thus a decrease in soil CO₂ flux [24]. In boreal forests, the appearance of a moss layer provides an additional source of organic matter for the ecosystem. Some studies even show that, in the case of poor soil, the litter of vascular plants is more easily decomposed and consumed, while the organic matter of moss is not easily decomposed and instead accumulates in the soil. Therefore, the significance of moss layers is greater for soil C accumulation [56]. However, it has also been found that in boreal forests, lichen layers can lead to a decrease in soil organic matter content [28]. In addition, the moss layer also has an impact on the litter decomposition of vascular plants. Litter distributed below the moss layer will accelerate the decomposition, while litter distributed above the moss layer will slow down the decomposition [57]. In other words, the moss layer can inhibit the decomposition of vascular plants by intercepting their litter, thus leading to the accumulation of soil organic matter. Furthermore, after the occurrence of wildfires, the ground cover is largely destroyed; if there is no other ground cover, there will be strong erosion, leading to the loss of organic matter, while moss will rapidly form a biological crust, increasing the surface runoff but significantly reducing the loss of sediment and organic matter [58]. The drying and rehydration of moss due to drought and precipitation will lead to the loss of some C in moss tissues, which will be leached into the soil by precipitation and enter the soil C cycle, increasing the soil C content [59].

2.2.2. Effects of Cryptogam on Soil Nitrogen Content and Availability

Similar to soil C, N in soil is also mainly derived from living plant secretions and dead residues [51], and also somewhat from atmospheric N deposition [60]. Thus, similar to soil C, in harsh environments such as deserts [15,18], sandy lands [14], drylands [52],

karsts [61,62], waste tailings [53], and high-altitude [55] regions, cryptogam secretions and dead residues are the most important sources of soil N. Therefore, the soil covered by cryptogams has a higher TN content. In forest ecosystems, due to the absorption and retention of N by moss, the soil will reduce the acquisition of N in a short period of time, but this part of N will still be returned to the soil after the death of moss [63]. As such, from a long-term perspective, moss reduces the loss of N in the ecosystem and is conducive to the accumulation of soil N. In addition, in nitrogen-poor boreals, feather mosses secrete chemicals to attract nitrogen-fixing cyanobacteria as a source of N [64]. When feather mosses die and decompose, the obtained N is released into the soil. Studies of boreal forest burned areas have found that moss layers accelerate the decomposition rate of vascular plant litter and cause more N to be retained in the litter [65], promoting N accumulation in ecosystems. In urbanized areas, moss can absorb excess N in the air and soil, forming a small N sink to prevent N loss or N pollution [66]. In the face of environmental erosion, moss-covered soils can maintain a higher TN content [67].

In addition to the effects on soil TN content, cryptogam also exerts important effects on the transformation, availability, and form of N in soil. In desert areas, moss crust contributes to the transformation of soil N, resulting in increased contents of NH_4^+ -N and NO_3^- -N in the soil, but lichen crust does not improve the transformation of N [16,25]. In addition, some studies have found that the influence of moss crust on the content of various forms of N in the soil in desert areas is regulated by water conditions. In the case of drought, it leads to the accumulation of NH_4^+ -N. Conversely, in humid environments, it increases the content of NO_3^- -N in the soil [68]. In karst areas, in addition to increasing soil TN, NH_4^+ -N, and NO_3^- -N contents, moss crust can also significantly increase urease activity, soil microbial biomass, and diversity [61]. If the moss crust is destroyed and removed, this positive effect quickly fades [20,21]. This suggests that moss has the potential to increase soil N availability in karst areas. In temperate forests, mosses have been found to favor soil NH_4^+ -N accumulation but reduce soil nitrate nitrogen content [69], and the effect of moss on soil nutrient content is strongly influenced by seasons (monsoon season and winter seasons are significantly different) [70]. In boreal forests, mosses promote NH_4^+ -N accumulation, while lichens increase NO_3^- -N content in soil [28]. In the Loess Plateau area of China, researchers have not only found that the soil AN content under the moss layer is higher [71] but also that the artificial cultivation of the moss crust can directly increase soil AN [72]. However, in subpolar birch forests, moss causes a decrease in soil temperature and prevents atmospheric nitrogen deposition into the soil, resulting in decreases in soil nitrogen availability, limiting nitrogen cycling, and ultimately leading to a decrease in soil NH_4^+ -N and DON content [29].

2.2.3. Effects of Cryptogam on the Content and Availability of Phosphorus, Potassium and Micronutrients in Soil

P in soil mainly comes from the weathering of parent material [73], and the dynamics of P in soil mainly include weathering generation, absorption, and utilization by plants, in addition to adsorption and loss [74]. Similar to P, K in soil is also mainly derived from the weathering of the parent material, but the difference is that K in soil is more easily lost via precipitation than P [75]. In desert ecosystems, due to the lack of parent material, lichen or moss crust usually increases TOC and TN, but not TP and TK, contents in soil [14–17,26,76]. Only several studies have found that biological soil crust increases soil TP [18,27] and TK [19,23] contents. In rocky desertification areas (including karst areas) with sufficient parent material, moss crust is found to increase soil TP [20,21,61] and TK [22] contents. In both stand and burned areas of boreal forest, mosses accelerate the decomposition rate of vascular plant litter but reduce the loss of P in litter [57,65], thereby alleviating the loss of P in the ecosystem and facilitating its accumulation in the soil. Moss layers are also found to be conducive to the accumulation of soil TP and TK in grasslands [77]. In the face of erosion, soil covered by moss also retains a higher TP and TK content [67]. In general, cryptogam can promote the accumulation of TP and TK in soil, possessing a better-promoting effect

than that of lichen [23]. These studies suggest that the effect of cryptogams on soil P and K content is mainly achieved by influencing the weathering of the parent material and the decomposition of litter.

Cryptogams have more influence on soil P and K availability than on TP and TK. In desert scenarios, lichen and lichen crust significantly increase soil AP [15,17,26] and AK contents [18,27]. However, this effect is limited to the topsoil (no more than 5 cm deep). In addition, moss has been found to increase soil PO_4^{3-} -P content in deserts [76]. Other studies have shown that in semi-arid deserts, the moss layer accumulates some AP in the dry season. When the rainy season comes, this part of AP will be leached into the soil by precipitation [31], resulting in an increase in soil AP content. However, in sandy land, moss can only increase AK content and decrease AP content in surface (0–2 cm) soil [14]. In drylands, both lichen and moss have enhanced soil acid phosphatase activity [52], suggesting that both of them have the potential to improve soil P availability. Moss also enhances the availability of soil P and K in rocky desertification areas [22,78]. Mosses and lichens have been found to improve soil P availability in grasslands and high-latitude areas [54,77].

To sum up, in most ecosystems, cryptogams play a role in improving the content and availability of soil C, N, P, and K (Table 2), and there are important interactions between these elements in the soil. For example, cryptogam plants lead to increases in soil N content and availability, elevating plant primary productivity and providing more organic carbon sources for the soil. However, soil N has a complex effect on C accumulation. Some studies found that more N would inhibit soil C accumulation [79], while others found that soil N had a positive effect on soil C accumulation [80], or otherwise no effect [81]. From a long-term perspective, the enrichment of soil N will lead to the accumulation of soil C. It has also been found that the enrichment of P in the soil promotes the cycle of soil C and N and that increases in P will boost soil C sink and N sink [82]. We hypothesize that the effect of cryptogam plants on soil nutrient content may be caused by a combination of their direct impact and nutrient interaction.

Table 2. Effect of cryptogams on soil fertility.

Geomorphic Feature	Cryptogam Species	Cryptogams Covered Soil Fertility Percent Change Compared with Bare Soil (%)					Reference
		SOM	TOC	TN	TP	TK	
Sandland	Moss-dominated crust	+335.9–+118.3	—	+300–+200	+59.1–+17.4	–17.6––1.2	[14]
The Loess Plateau	Moss crust	+1011–+398	—	+189	ns	—	[15]
Desert	Moss crust	+789.2	—	+233.3	+73.7	+830.8	[19]
Karst	Moss crust	—	+47.1	+63.9	+19.0	—	[20]
Desert	Moss crust	+183.5	—	+47.4	—	—	[25]
Greenhouse in desert	Moss crust	+748.4	—	—	—	—	[26]
Burned forest and sand mine	Natural moss layer	+375–+281	—	—	—	—	[28]
Abandoned pyritic mine tailings	<i>Campylopus schmidii</i>	+46.4	—	—	—	—	[53]
Sandland	Moss crust	—	+460	+364	+40	—	[55]
Karst	Moss crust	—	ns	+102.8	+83	—	[61]
The Loess Plateau	Moss crust	—	+160.8	+49.7	+12.3	—	[77]

+: cryptogams improve soil fertility; –: cryptogams reduce soil fertility; ns: cryptogams have no significantly effect on soil fertility.

3. Effects of Cryptogam on Vascular Plants Regeneration

Cryptogams have important and complex effects on vascular plant regeneration. In Xu's study, vascular plant coverage was significantly positively correlated with lichen coverage and negatively correlated with moss coverage, which seems to indicate that lichen is conducive to vascular plant regeneration, whereas moss obstructs its regeneration [6]. Ren et al. found that *Primulina tabacum* had better regeneration status in the area covered by the bryophyte *Gymnostomiella longinervis* [83]. It has also been shown that moss bedding has no significant effect on seed germination [84]. Research has found that the cryptogam

promotion of the regeneration of vascular plants increases the seed germination rate [85], promotes the establishment and growth of seedlings [86,87], and improves seedling survival rates [88]. The inhibitory effect on vascular plant regeneration was primarily demonstrated to be a reduced seed germination rate [89–91], prolonged germination time [92–94], and inhibited seedling growth [95]. Other studies have found that bryophytes can not only reduce germination rate and prolong germination time but also lead to the deterioration of seed water state [96], thus reducing seed germination potential. Deines et al. also found that lichen crusting reduces the ability of seedling roots to penetrate the soil [92], leading to seedling death due to a lack of access to water and nutrients. Some studies have found that the same cryptogams have completely opposite effects on the seed germination and seedling growth of the same vascular plant. Song et al. found through greenhouse experiments that the crust of cyanobacteria, lichens, and mosses inhibited the germination of *Ceratoides latens* and *Setaria viridis* seeds but promoted their seedling growth [97]. A study in the desert also found that biological crusts inhibited the germination of *Agriophyllum squarrosum*, *Eragrostis minor*, and *Grubovia dasyphylla* seeds but promoted seedling growth. The inhibitory effect of crust on seed germination can be alleviated by proper sand burial treatment [98].

Bryophytes have a “filtrating function” for the regeneration of native and exotic plant species. Some studies have shown that bryophytes have no effect on the seed germination of native vascular plants but significantly inhibit exotic species germination [99]. Hernandez’s research also showed that moss crust does not limit the emergence of native plants but can effectively resist the emergence of exotic species [100]. Under high soil moisture content in greenhouse conditions, the lichen-moss crust was found to inhibit the seed germination of both native plants and exotic plants. Conversely, in the wild natural environment, lichen-moss crust mainly inhibited the seed germination and seedling establishment of exotic species [101]. In Song’s study, lichen and moss crusts exerted an inhibitory effect on the seed germination of native plants. However, their inhibitory effect on exotic species was found to be stronger, and the destruction of crusts enabled invasion by exotic species [26]. This information seems to suggest that the cryptogam community is a natural biological barrier against invasion by exotic species, but the amount of relevant research is still limited.

3.1. Physical Barrier

Cryptogam often covers the surface of the soil like a “carpet”, prevents seeds and sunlight from reaching the soil, and then affects vascular plant regeneration. In a desert study, moss crust restricted seed entry into the soil and significantly reduced seed bank density (4–23 seeds per 0.005 m²). After the moss crust was destroyed, the seed bank density returned to bare soil level (>60 seeds per 0.005 m²) [32]. Briggs studied the germination ability of five plant seeds in different ground cover patches and found that the seeds with the largest size were significantly inhibited in germination because the moss layer prevented them from reaching the suitable substrate for germination, while the remaining seeds were small and could get through the moss layer. As such, germination was not affected [102]. Huber’s study also found that moss significantly inhibited the germination of grass seeds, with seed size directly proportional to the inhibition effect, but moss did not inhibit the growth of seedlings [103]. Guo’s research showed that moss layers not only accumulate more *Emmenopterys henryi* seeds than bare layers but also reduce the germination rate of seeds [104]. In Jeschke’s study, the physical barrier and shading effect of moss significantly inhibited seed germination and the seedling growth of four herbaceous plants [35].

3.2. Allelopathy

The allelopathic effect of cryptogams on vascular plants has been documented extensively. The effect of water extracts on vascular plant regeneration is often manifested as a high concentration of extracts inhibiting vascular plant regeneration, while a low concentration has the opposite effect. Moreover, lichens usually have a negative allelopathic effect on vascular plant regeneration. For example, Michel’s study found that high concentra-

tions (5–10%) of moss water extracts inhibited seed germination and seedling root growth, but low concentrations of moss water extracts promoted seed germination [33]. The low concentration of moss water extract (0.5–5 mg·mL⁻¹) improved the germination rate of *Picea crassifolia* seeds by inhibiting fungal infection of seeds, whereas the high concentration (50 mg·mL⁻¹) significantly inhibited seed germination [105]. In Sedia's study, lichen water extracts significantly inhibited seed germination in three species of vascular plants (*Pinus rigida*, *Schizachyrium scoparius*, and *Vaccinium pallidum*). The water extract of moss had no effect on seed germination [36]. There are many allelopathic substances in the extracts of cryptogam. For example, Basile et al. extracted 7 flavonoids from 5 species of moss and found that these 7 flavonoids inhibited the root growth of *Raphanus sativus* and led to changes in root morphology [106]. Using 3-Hydroxy-beta-ionone, an allelopathic substance found in *Rhynchostegium pallidifolium*, we discovered that 1–3 µmol·L⁻¹ of this substance resulted in a 46–64% reduction in the hypocotyl and root growth of *Lepidium sativum* [107]. The usnic acid present in *Cladonia* spp. lichen extracts also had significant allelopathic effects on vascular plants, having also been found to significantly inhibit the regeneration of *Abies balsamea* [38]. It also significantly inhibited the above-ground and below-ground growth of half-year *Pinus banksiana* seedlings and still inhibited the root development of 2-year seedlings [108]. Phenolic substances are also widely found in cryptogams [109], in which phenolic acids exert significant allelopathic effects on vascular plants. When the concentration of phenolic acids (including p-hydroxybenzoic acid, protocatechuic acid, syringic acid, vanillic acid, gallic acid, salicylic acid, ferulic acid, p-coumaric acid, and caffeic acid, etc.) was higher than 20 mmol·L⁻¹, seed germination was significantly inhibited. However, 5–20 mmol·L⁻¹ phenolic acid had no significant effect on seed germination [110]. In soil, phenolic acids above 50 µg·g⁻¹ begin to inhibit vascular plant regeneration [111].

3.3. Cryptogam Indirectly Affects Vascular Plant Regeneration by Regulating Soil Conditions

A large number of studies have found that cryptogam affects the regeneration of vascular plants by regulating soil water status. In the absence of other water sources in areas with <500 mm annual precipitation, cryptogams can inhibit vascular plant regeneration by reducing soil water content. For example, in sandy environments, natural lichen and bryophyte crusts limit the regeneration of *Artemisia ordosica* by reducing soil water content [112]. Studies in semi-arid regions have also found that moss crust reduces soil water content, thereby inhibiting *Artemisia ordosica* regeneration [4]. A study of *Echinops gmelinii* regeneration in the Tengger Desert showed that, although moss crust significantly increased soil nutrient content (TOC, TN, TP, and TK), the regeneration capacity was still decreased, an effect caused by the moss-based redistribution of soil water [19]. However, when the annual precipitation was higher than 600 mm or there was artificial irrigation, cryptogams all had the effect of increasing soil water content to promote vascular plant regeneration. For example, in boreal forests with annual precipitation of more than 1000 mm, moss layers created a better soil water and temperature environment, which promoted the regeneration of *Abies balsamea* [38]. Researchers also found in evergreen broad-leaved forests that the moss layer is conducive to the accumulation of soil water and nutrients, thus promoting the regeneration of vascular plants [113]. In a study in the Tengger Desert in China, the same artificial irrigation was applied to soils with different biological crusting, and we found that moss crust improved the ability of soil to capture seeds. Due to the fact that moss crust limits water infiltration, the topsoil has a higher water content and promotes the germination of captured seeds. Moreover, the longer the moss crust development time, the better the soil water condition is and the higher the germination rate of seeds will be [114,115]. Videla separately designed the arid and humid environmental conditions in the greenhouse experiment, finding that moss only promoted the growth of *Leptochloa crinita* in the humid environment due to increasing soil moisture [68]. In greenhouse experiments, moss promoted the development of *Populus tremula*, *Salix caprea*, and *Betula pendula* due to their ability to hold soil water for longer [37]. In addition, some studies found that the effect of moss on soil water content depends on the height and density of moss. In the

mid-altitude mountain area with 437 mm of precipitation, excessive moss height (>5 cm) or density (>50%) will significantly reduce soil water content and inhibit vascular plant regeneration. However, low moss height or density will increase soil water content and promote vascular plant regeneration [34]. In addition, some studies have found that the effect of moss on soil water content depends on the height and density of the moss. In the mid-altitude mountain area with 437 mm of annual precipitation, excessively tall (>5 cm) or dense (>50%) moss will significantly reduce soil water content and inhibit vascular plant regeneration. However, low moss height or density will increase soil water content and promote vascular plant regeneration [34]. In addition, as mentioned above, cryptogams tend to lead to increased soil nutrient content and availability, providing more nutrients for vascular plant growth and promoting vascular plant regeneration. In greenhouse experiments, lichen crust promotes seed germination and the seedling growth of *Bromus tectorum* by increasing soil fertility [17]. In a study of the regeneration of two native species and one exotic species in different bio-crust soils, lichen and moss crusts 2343 were found to increase soil nutrient content and promote seedling growth [26]. In deserts, moss crust improved soil fertility and led to increased seed germination rates and seedling growth for *Leptochloa crinita* [68]. In addition, Pace's research also found that feather moss and *Sphagnum spp.* have different effects on seedling growth due to their different effects on soil nutrient availability [116].

3.4. Other Effects

In addition to the above three cases, other studies found a competitive relationship between cryptogam and vascular plants. Greenhouse experiments showed that the moss *Didymodon tophaceus* significantly improved the seed germination, seedling growth, and individual reproduction of the herb *Delphinium uliginosum*. However, in the later life stages of *Delphinium uliginosum*, *Didymodon tophaceus* exerts a competing effect on it [39]. In Stuiver's study, when the biomass of the four mosses reached its highest level, the growth of *Pinus sylvestris* seedlings was significantly reduced due to the competition between seedlings and moss for light. Additionally, the height and above-ground quality of the seedlings increased. The morphologically taller mosses *Hylocomium splendens* and *Polytrichum commune* competed with *Pinus sylvestris* the most intensely [117]. In addition, there are also some reports that cryptogams inhibit vascular plant regeneration in other ways, such as lichen. This prevents ectomycorrhiza from infecting seedling roots, leading to seedling stunting [36]. The decreasing effect of cryptogams on soil temperature will also reduce the accumulated temperature of the site environment, thus shortening the growing season of *Picea crassifolia* and limiting its regeneration [34]. It was also found that moss crust alleviates the effects of climate change on the establishment of vascular plant seedlings in the alpine forest line region. This limits the expansion of forest lines caused by climate warming [118]. Mosses in the desert have also been found to significantly reduce the reproductive capacity of *Echinops gmelinii* individuals, thereby limiting their regeneration ability [19]. To sum up, physical barriers, allelopathy, regulating soil conditions, competition, inhibiting ectomycorrhiza development, and reducing plant reproductive capacity are the ways in which cryptogams affect vascular plant regeneration (Figure 1).

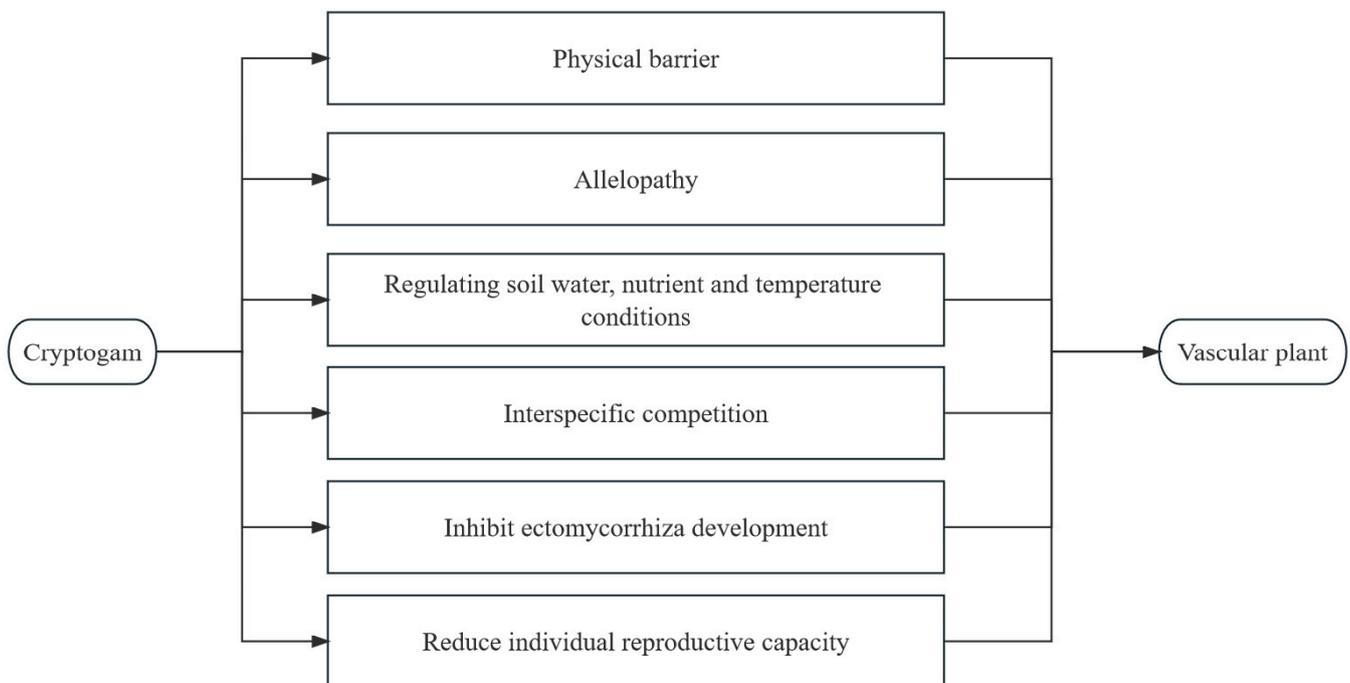


Figure 1. Effects of cryptogam on vascular plants regeneration.

4. Challenges and Opportunities

Through a discussion of the last two decades of studies with cryptogam, we found that, in the absence of artificial irrigation and other sources of water, there appears to be a boundary between the average annual precipitation of 500–600 mm: moss promotes the accumulation of soil water in areas where annual precipitation is above this value, whereas cryptogams accelerate soil water loss in areas with levels below it. Moreover, the effect of cryptogam on soil water content will further affect the regeneration of vascular plants. Thus, we might ask: what is driving this phenomenon whereby cryptogam plants intercept the thin precipitation in arid regions? Is it the regulation of evaporative dispersion by cryptogam? Or changes in soil structure caused by cryptogam? Perhaps something else? This remains an open question.

A large number of studies have shown that cryptogams (or their biological soil crust) can improve the fertility of soil and the availability of nutrients (TOC, TN, TP, TK, and micronutrients) in deserts, sandy land, drylands, karst, waste tailings, burned land, high-latitude and high-altitude zones, and other harsh environments. However, there are only a few studies on the effects of cryptogam plants on soil nutrient cycling and land fertility in grasslands, forests, and other ecosystems. It has to be said that the effects of cryptogam plants on soil nutrients have been neglected in these areas. Since soil nutrients are closely related to plant growth, it is necessary to comprehensively and systematically study the effects of cryptogam on soil nutrient content in these ecosystems.

Now studies have found that cryptogam increases the ability of ecosystems to resist invasion by exotic species. However, these studies have generally occurred in ecologically fragile areas such as deserts [26], burned land [95], and semi-arid areas [96,97]. In 2019, there is limited research on whether cryptogam can inhibit the invasion of exotic species in stable ecosystems such as grasslands, woodlands, and even farmland.

5. Conclusions

Cryptogams are widely distributed across the earth. Although small in size, the strength of their stress resistance has rendered them the dominant vegetation in many harsh environments where vascular plants cannot live. As such, they play strong ecological roles in these ecosystems. In regions with low annual precipitation (<500 mm), cryptogam

causes a decrease in soil water content. Conversely, in places with high annual precipitation (>600 mm) or artificial irrigation, they improve soil water content. A large number of studies have confirmed that cryptogams increase the amounts of soil OM, TOC, TN, TP, TK, and micronutrients in harsh environments and improve their availability. At present, there are limited studies on the soil fertility of vascular plants in grassland and forest ecosystems. Several studies have found that they can increase soil nutrient content in grassland and forest ecosystems, but there are also studies that have found that lichens can reduce soil OM content [28]. The effects of cryptogam on vascular plant regeneration are mainly caused by their physical barrier, shading, allelopathy, soil water content and nutrient regulation, and competition. Some studies have also found that cryptogams affect vascular plant regeneration by preventing ectomycorrhizal infection of vascular plant roots, regulating environmental temperature, and affecting individual plant reproduction ability. In addition, cryptogam can resist the invasion of exotic species into fragile ecological areas.

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